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Changes in connectedness over time in alternative sheep sire referencing schemes^{1,2}

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ABSTRACT: A statistic to measure the level of connectedness achieved among flocks would help producers to assess the risk of comparing EBV of animals from different flocks. The objectives of this research were to evaluate the pattern of change over time in selected connectedness measures and to determine how effectively these measures quantify the level of risk due to potential bias in EBV comparisons across production units. Connectedness was evaluated using simulated sheep populations, with connections established using sire referencing schemes (SRS). Pedigree and performance data for a single trait with a within-flock heritability of 0.25 were simulated (50 replications) for 15 flocks with 40 to 140 ewes per flock. Genetic means for each flock were sampled from a normal distribution with mean 0 and SD equal to the trait's genetic SD. After 10 yr of random mating, flocks had opportunity to join a SRS and selection began for the simulated trait. Yearling rams were chosen as reference sires randomly from the top one-sixth of the population ranked on BLUP EBV. Every year, in each flock, 3 reference sires were mated to 10 ewes each. Six sire referencing scenarios (including no SRS) and 2 sources of nonreference

sires were simulated. Connectedness was measured in 2 ways: (i) as the average prediction error correlation (r_{ij}) of the flock genetic means (flock r_{ij}) or the EBV for the current crop of ram lambs (lamb r_{ij}) or (ii) as the average scaled prediction error variance of differences (PEVD) in flock genetic means (flock PEVD) or in lamb EBV in the current crop of ram lambs (lamb PEVD). Flock r_{ij} increased linearly in all scenarios while SRS was underway and leveled off if the flocks discontinued SRS. Lamb r_{ij} increased rapidly as soon as SRS began but decreased substantially if the flocks discontinued SRS. Behavior of flock PEVD and lamb PEVD measures were similar but in the opposite direction (i.e., PEVD decreased with increasing r_{ij}). Within scenarios, both flock r_{ij} and flock PEVD had a nonlinear relationship with bias in comparing animals across flocks. However, only flock r_{ij} exhibited a consistent relationship across simulation scenarios. When flock r_{ij} reached 0.05 and 0.10, approximately 20 and 10%, respectively, of the bias due to initial differences in flock genetic means remained. These levels of flock r_{ij} are suggested as benchmark levels for minimizing the risk of comparing animal EBV among units.

Key words: connectedness, genetic evaluation, simulation, bias, sheep

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INTRODUCTION

Sire referencing schemes are cooperative breeding programs where genetic links between flocks are

formed by sharing rams among flocks. Participation in these schemes has been clearly shown to accelerate rates of genetic gain (Hanocq et al., 1996; Roden, 1996; Lewis and Simm, 2000). These schemes improve the accuracy of across-flock genetic comparisons (Foulley et al., 1983) and may reduce rates of inbreeding (Lewis and Simm, 2000; Kuehn et al., 2007). Biases in EBV due to differences in genetic means among flocks decrease as connections among management units in schemes are established (Hanocq et al., 1996; Kuehn et al., 2007).

Despite these benefits, restrictions such as AI mating and commitment to use reference sires may limit producer participation in sire referencing schemes, at

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least for extended periods. Still, it is useful for producers to know the relative rank of their animals in the population for effective genetic improvement using outside sources of germplasm. If producers are not sufficiently connected to other management units there is risk of bias in across-unit genetic comparisons. Therefore, it would be useful to have a measure of the risk of potential bias when comparing animals across units.

Various connectedness measures have been proposed including the average prediction error of EBV differences across units (Kennedy and Trus, 1993) and the correlation of prediction errors across units (Lewis et al., 1999, 2005). These measures are currently used in Canada and the United Kingdom to measure connectedness. However, the behavior of these measures over time and relative to biases due to different unit genetic means has not been well established. The objectives of this study were to use simulation to evaluate patterns of change over time in selected connectedness measures in sire referencing schemes and determine how effectively these measures quantify the level of risk due to potential bias in EBV comparisons across production units.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were simulated data as described in the next section.

Simulation

Simulation Models. Data sets were simulated using a modified version of the stochastic simulation of Lewis and Simm (2000). Specific parameters defining mating, reproductive, and survival characteristics were described by Kuehn et al. (2007). Fifteen flocks ranging in size from 40 to 140 breeding ewes were simulated, for a total of 1,030 breeding ewes per year. A single trait with a moderate within-flock heritability of 0.25, typical of growth and yield traits, was simulated for each animal. To create genetic differences among flocks, breeding values for base animals were obtained from normal distributions, with genetic means μ_j for flock j and a common within-flock additive variance (σ_a^2) of 0.25. Values of μ_j for each flock were likewise sampled from a normal distribution with mean zero and variance 0.25. Breeding values and phenotypes for all animals were derived using the procedures of Kuehn et al. (2007).

Each flock underwent 10 yr of random selection followed by 15 yr of selection on the simulated performance trait. Rams selected from across the scheme as well as rams selected for use within their respective flocks were selected at random from the top one-sixth of their respective pools as ranked by BLUP EBV. Ewes still alive after their fourth lambing were culled. Enough ewe replacements were selected each year by

BLUP EBV to maintain a constant flock size, resulting in an average replacement rate of 26%.

Simulation Scenarios. Connectedness was measured across flocks participating in several types of cooperative breeding schemes. Each scheme was replicated 50 times. Two schemes were used as baselines for comparison: (i) all flocks participating in an AI sire referencing scheme for all 15 yr of selection, or (ii) flocks that remained autonomous for all 15 yr of selection (no connections), with only within-flock selection. For the AI sire referencing scheme, 6 rams were chosen as a team from the 15 flocks and made available as reference sires. Half of the team was replaced each year. Each flock randomly selected 3 reference sires from the team and mated each sire to 10 ewes. Flocks were allowed to reuse 1 reference sire in consecutive years while participating in the scheme.

In addition to the baseline schemes, 4 other breeding schemes were simulated: 2 schemes involving termination of sire referencing after 5 or 10 yr, with the flocks remaining autonomous thereafter; flocks with sporadic participation in sire referencing; and natural service (as opposed to AI) sire referencing, which involved exchange of rams among flocks and a reference sire pool of 45, rather than 6, rams. Changes in connectedness and bias in estimation of breeding values across flocks were compared for these scenarios. Details on the specific assumptions of the sporadic and natural service sire referencing schemes can be found in Kuehn et al. (2007).

All 6 scenarios were simulated with 2 strategies for acquisition and use of rams other than the reference sires. In the first case, half of the flocks mated their excess ewes to unrelated purchased rams with no pedigree or performance data, and the rest of the flocks mated on average one-half of their excess ewes to purchased rams and one-half to their own homebred rams. Breeding values for the purchased rams were sampled from a normal distribution with mean $0.8 \theta_i$ and variance 0.25, where θ_i is the mean true breeding value of the overall scheme in year i . The value of 0.8 was chosen to reflect the genetic distance between flocks practicing across-flock vs. within-flock selection on BLUP EBV (Lewis and Simm, 2000).

The first sire usage strategy reflects the level of purchased animal use in flocks that participate in sire referencing in the United Kingdom (Lewis and Simm, 2000) and henceforth will be referred to as the outside sire strategy. In the second sire usage strategy, all flocks used only their own homebred sires in addition to the required reference sires. Although not likely in practice, this strategy provided a contrast to the outside sire strategy. This sire usage strategy will henceforth be referred to as the homebred only sire strategy. With these 2 sire use strategies (outside vs. homebred) and the 6 breeding schemes, 12 scenarios were explored.

The scenarios considered were the same as those used in Kuehn et al. (2007) to evaluate the effective-

ness of natural service and discontinuous sire referencing schemes at removing bias due to differing flock genetic means compared with AI sire referencing. Their results suggested that bias decreased at a decreasing rate as sire referencing schemes progressed. Bias was dramatically reduced after 5 yr with natural service and AI sire referencing, and after 10 yr with sporadic participation in the AI scheme. For this study, several connectedness measures were compared to determine whether the loss of bias could be predicted using these statistics.

EBV Prediction Model

An animal model with full relationships was used to derive EBV used for selection within the simulation scenarios. Fixed effects included flock, year, sex, and number of lambs born in a litter. In the outside sire strategies, fixed genetic groups, defined by birth year of sires introduced from outside the scheme, were also fitted. Further details on the model fitted are available in Kuehn et al. (2007).

Summary Statistics

Connectedness between groups of animals has traditionally been measured using functions of the inverse of the coefficient matrix (**C**; Foulley et al., 1992; Kennedy and Trus, 1993; Laloë, 1993):

$$\mathbf{C} = [\mathbf{Z}'\mathbf{M}\mathbf{Z} + \lambda\mathbf{A}^{-1}],$$

where **M** is the fixed effect absorption matrix, λ is the ratio of residual and additive variances (σ_e^2/σ_a^2), and **A** is the numerator relationship matrix. The inverse elements of **C**, multiplied by σ_e^2 , are the prediction error (co)variances of the EBV.

For this study, 2 connectedness measures based on functions of prediction error were calculated for each year of selection in each simulated data set. The first measure was the connectedness correlation (Lewis et al., 1999, 2005):

$$r_{ij} = \frac{\text{PEC}(\hat{u}_i, \hat{u}_j)}{\sqrt{\text{PEV}(\hat{u}_i)\text{PEV}(\hat{u}_j)}},$$

where **PEC** = prediction error covariance and **PEV** = prediction error variance; and \hat{u}_i and \hat{u}_j are EBV of animals i and j , respectively. The connectedness correlation was calculated and averaged each year for all pairs of ram lambs born in different flocks across all 15 flocks (lamb r_{ij}). This statistic was also calculated yearly on a flock mean basis:

$$\text{flock } r_{ij} = \frac{\text{PEC}(\hat{\bar{u}}_i, \hat{\bar{u}}_j)}{\sqrt{\text{PEV}(\hat{\bar{u}}_i)\text{PEV}(\hat{\bar{u}}_j)}},$$

where $\hat{\bar{u}}_{i(j)}$ is the mean breeding value of all animals recorded in flock $i(j)$ since recording began. This flock connectedness correlation (flock r_{ij}) was shown by Lewis et al. (1999, 2005) to have a strong relationship with bias arising from different flock genetic means, with higher r_{ij} values corresponding with less bias. Flock r_{ij} is thus a measure of connectedness for all animals in the pedigree, whereas lamb r_{ij} is descriptive of the current generation.

The second connectedness statistic calculated was the scaled PEV of the difference (**PEVD**) in EBV between animals in different flocks:

$$\begin{aligned} \text{scaled PEV}(\hat{u}_i - \hat{u}_j) = \\ [\text{PEV}(\hat{u}_i) + \text{PEV}(\hat{u}_j) - 2\text{PEC}(\hat{u}_i, \hat{u}_j)]/\sigma_a^2. \end{aligned}$$

Like the connectedness correlation, this statistic was calculated each year both for all pairs of ram lambs from different flocks (lamb PEVD) and for the mean EBV of all animals in each flock since recording began (flock PEVD). Scaling the PEVD by the additive variance (σ_a^2) allowed this statistic to be expressed without units. The average PEVD of EBV across management units was first suggested by Kennedy and Trus (1993) as the most appropriate measure of connectedness because it measures the inherent risk in comparing these animals. Kennedy and Trus hypothesized that a lower average PEV corresponds to a reduced risk of comparisons across units.

The ideal connectedness statistic would measure the risk of potentially biased EBV comparisons across flocks due to different initial flock genetic means. Therefore, after the behavior of these statistics over time was assessed, candidate connectedness measures were plotted relative to the bias remaining in the system due to simulation of different initial flock genetic means. As in Lewis et al. (1999), to quantify the bias associated with comparisons of animals between flocks, a contrast (L_{ij}) was calculated for all pairs of rams lambs produced in each year:

$$L_{ij} = (u_i - u_j) - (\hat{u}_i - \hat{u}_j),$$

where u_i and u_j are the true breeding values of animals i and j , respectively. Ram lambs were chosen for these contrasts because they were the candidates for future reference and homebred sire selection. The statistic was squared and averaged for pairs of ram lambs across flocks, resulting in a measure of the mean squared error (**MSE**) of prediction of differences in breeding values of ram lambs born in different flocks. The MSE is the sum of the PEVD and the squared bias in this predicted difference. In addition to the between-flock MSE (**MSE_B**), the average squared L_{ij} of pairs of lambs born within the same flock was also computed. This within-flock MSE (**MSE_W**) was assumed free of bias since the lambs were born in the same flocks and, hence, would only consist of the PEV

of EBV differences. Therefore, the difference between MSE_B and MSE_W estimates the squared bias due to different flock genetic means.

In their previous study, Kuehn et al. (2007) found that the amount of bias in year zero of selection was dependent on whether outside sires were allowed or excluded. When both homebred and outside sires were used, MSE_B averaged 0.50 at year zero; when no outside sires were allowed, MSE_B averaged 0.83. Across all years, MSE_W remained at an average level of 0.27. Because the beginning level of bias in across-flock breeding value differences was strategy-dependent, a percentage decrease from the original level of bias was calculated for this study to compare with the connectedness measures as:

$$\% \text{ Bias} = \frac{MSE_{Bi} - MSE_W}{MSE_{B0} - MSE_W} \times 100 = \frac{MSE_{Bi} - 0.27}{MSE_{B0} - 0.27} \times 100,$$

where MSE_{B0} is the mean squared across-flock L_{ij} in selection year 0 of the current simulation replicate and MSE_{Bi} is the mean squared L_{ij} in selection year i .

RESULTS

Connectedness Statistics

Connectedness Correlations. As selection and sire exchange across flocks began, the value of both of the correlation connectedness statistics (lamb r_{ij} and flock r_{ij}) increased in the sire referencing scheme scenarios (Figure 1, Table 1). When no sire referencing was undertaken, both lamb and flock r_{ij} necessarily remained at zero. Lamb and flock r_{ij} in continuous AI sire referencing and in AI sire referencing for 5 or 10 yr were expected to be the same after 5 yr of selection; the same was expected for continuous AI sire referencing with the AI sire referencing for 10 yr scenario after 10 yr of selection. The observed differences were within the standard error. The magnitudes of lamb and flock r_{ij} differed by a factor of approximately 10, indicating a greater level of confidence in estimates of difference in mean EBV between flocks than in estimates of difference in individual lamb EBV. This result was expected because means are less variable than individual predictions.

Lamb r_{ij} increased rapidly the first year after breeding schemes began and thereafter increased at a slow but constant rate as long as the schemes remained in effect. Lamb r_{ij} increased most rapidly in AI sire referencing schemes, whereas in sporadic and natural service schemes lamb r_{ij} increased less rapidly. When sire referencing was discontinued after 5 (Figure 1) or 10 yr, lamb r_{ij} then rapidly decreased and then slowly declined thereafter. Unlike lamb r_{ij} , the rate of increase in flock r_{ij} was generally constant from year to year as long as flocks continued to participate in the scheme. Also, flock r_{ij} increased more rapidly under natural service sire referencing than AI sire referenc-

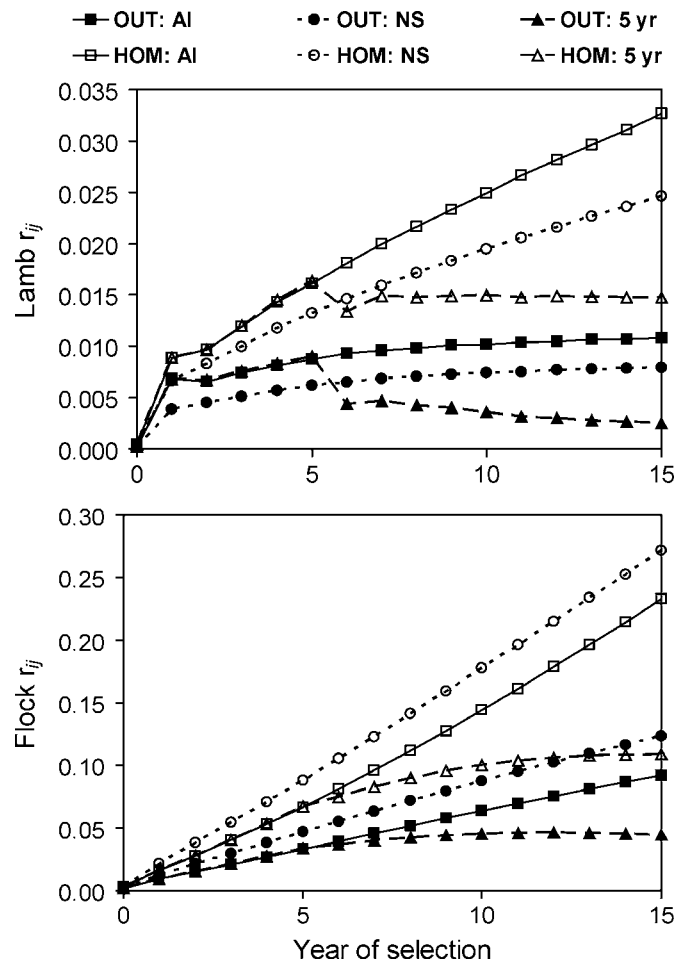


Figure 1. Average lamb and flock connectedness correlation (r_{ij}) between 15 flocks over 15 yr of selection for 3 different breeding schemes: AI sire referencing (AI), natural service sire referencing (NS), and sire referencing for 5 yr followed by 10 yr where flocks are independent (5 yr). Flocks were allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

ing. In contrast to the case with lamb r_{ij} , if flocks discontinued reference sire matings after 5 or 10 yr, flock r_{ij} did not immediately decrease. Instead, the level of flock r_{ij} increased at a decreasing rate, eventually reached a peak, and then slowly declined.

Both of the connectedness correlation measures increased approximately twice as fast when only homebred vs. some outside sires were used for nonreference sire matings. The introduction of nonpedigreed sires dilutes the average relationship between animals in different flocks, which results in a lower level of prediction error covariance between them and, therefore, lower connectedness correlations.

Prediction Error Differences. As expected, both lamb and flock PEVD decreased as soon as group breeding schemes began (Figure 2, Table 2). If no scheme was implemented, lamb and flock PEVD slowly increased over all 15 yr, probably due to increased

Table 1. Levels of lamb and flock connectedness correlations (r_{ij}) after 5, 10, and 15 yr of selection under different types of sire referencing schemes and different levels of outside sire use

Source of nonreference sires	Breeding scheme	Lamb r_{ij} ¹			Flock r_{ij} ¹		
		5	10	15	5	10	15
Outside allowed	AI continuous	0.009	0.010	0.011	0.033	0.064	0.092
	AI 5 yr	0.009	0.004	0.002	0.033	0.045	0.045
	AI 10 yr	0.009	0.011	0.004	0.034	0.065	0.079
	AI sporadic	0.006	0.007	0.008	0.025	0.048	0.069
	NS ² continuous	0.006	0.007	0.008	0.047	0.087	0.123
Homebred only	AI continuous	0.016	0.025	0.033	0.067	0.144	0.233
	AI 5 yr	0.016	0.015	0.015	0.067	0.100	0.109
	AI 10 yr	0.016	0.025	0.023	0.067	0.144	0.194
	AI sporadic	0.012	0.021	0.028	0.050	0.110	0.178
	NS continuous	0.013	0.019	0.025	0.088	0.178	0.271

¹SE for lamb r_{ij} and flock r_{ij} were < 0.0003 and < 0.003, respectively.

²NS = natural service.

levels of inbreeding and average relationship within the independent flocks. Differences in lamb and flock PEVD in continuous AI sire referencing and AI sire referencing for 5 or 10 yr were expected to be the same after 5 yr of selection; the same was expected at yr 10 for the 10-yr scenario. Once again, differences between these scenarios were within the standard error.

Patterns of lamb PEVD mirrored those in lamb r_{ij} in that lamb PEVD dropped quickly in the first year after the breeding scheme began followed by a gradual decline thereafter. If flocks discontinued participation in a scheme after 5 or 10 yr, lamb PEVD rapidly increased the following year. When participation in the scheme was sporadic, the rate of decrease in lamb PEVD was slower than when flocks continually participated. Similar to lamb r_{ij} , gains in connectedness as measured by lamb PEVD were slower for natural service sire referencing than for AI sire referencing. Higher values for lamb PEVD in natural service as compared with AI schemes indicate that the accuracies of comparisons of lambs across flocks were lower with use of natural service compared with AI reference sires. The average level of lamb PEVD after 15 yr ranged from 1.108 with AI sire referencing and no outside sires allowed to 1.460 with no reference sire use and no outside sires allowed.

Both lamb and flock PEVD values were higher at yr 0 if use of outside sires was not allowed. As reported by Kuehn et al. (2007), this discrepancy was likely due to the higher inbreeding in these scenarios (5.2 and 2.2%, respectively) after 10 yr of random mating but before selection. Inbreeding and within-flock relationships increase the additive variance between flocks; the upper limit of PEVD is proportional to the between-flock additive variance. Once breeding schemes were initiated, flock PEVD dropped more rapidly in scenarios with no outside sires, eventually converging with the flock PEVD from the other scenarios. As found when comparing flock to lamb r_{ij} , natural service sire referencing was no longer disadvantageous with re-

gard to connectedness relative to AI sire referencing based on flock PEVD. As expected, declines in flock PEVD were slower with sporadic participation in the scheme, and flock PEVD increased slightly if flocks discontinued participation in the scheme altogether.

Connectedness Measures Relative to Bias

Kuehn et al. (2007) illustrated that for all of these simulated breeding schemes, bias decreased at a decreasing rate as the schemes progressed. Their results show that the MSE of across-flock comparisons of lamb EBV asymptotically approach the MSE of the within-flock comparisons over time, indicating a reduction in bias in the across-flock genetic evaluations. Bias continued to decline over time and did not increase in cases where flocks discontinued sire referencing after 5 or 10 yr. Therefore, in choosing a candidate connectedness measure, it was important that the statistic was monotonic as years of selection increased. From the 4 measures described, flock r_{ij} and flock PEVD fit this criterion and were plotted against the percentage reduction in bias due to differing flock means in Figures 3 and 4, respectively.

In Figure 3, the percentage decrease in bias relative to flock r_{ij} is shown. Points on the lines represent averages for both statistics in each year. Because bias declines as connectedness accumulates, points on the figure associated with higher r_{ij} values correspond to more years of sire referencing. Regardless of whether outside sires were allowed, the percentage of bias decreased as flock r_{ij} increased, but both the percentage of bias explained ($1 - \% \text{ bias}$) and flock r_{ij} were higher when outside sires were not used. The pattern was more variable among scenarios when outside sires were used, but the relationship between bias and flock r_{ij} was reasonably consistent. When flock r_{ij} was 0.05, the remaining bias was around 20%, and when flock r_{ij} was 0.10, the bias decreased to less than 10%. It was difficult to extrapolate the relationship further because bias asymptotes at about 3%.

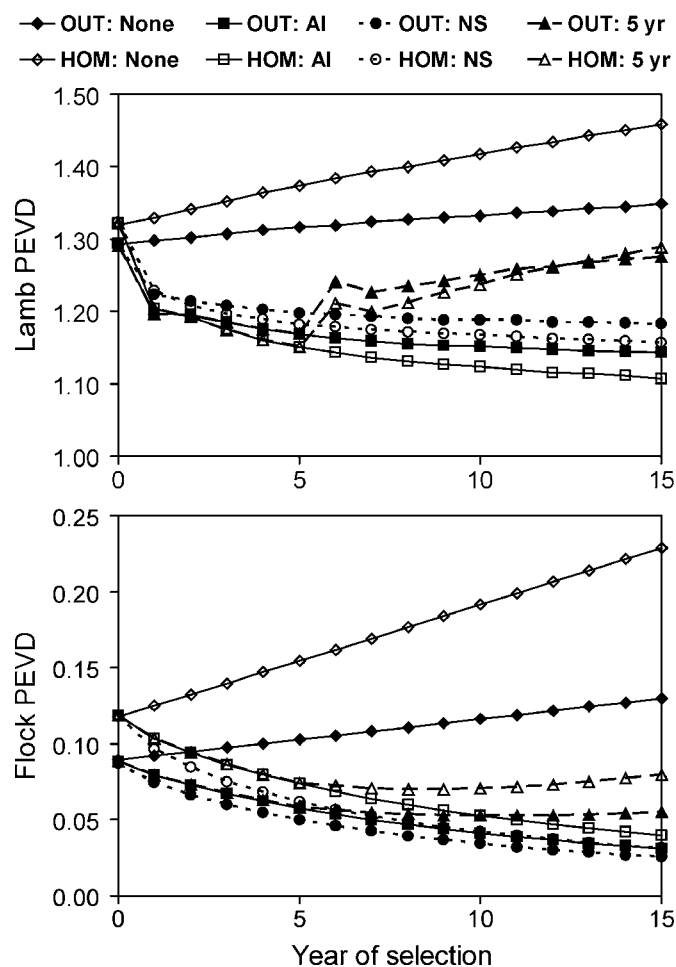


Figure 2. Average prediction error of differences (PEVD) in lamb EBV and flock mean EBV between 15 flocks after over 15 yr of selection for 4 different breeding schemes: no reference sire use (None), AI sire referencing (AI), natural service sire referencing (NS), and sire referencing for 5 yr followed by 10 yr where flocks are independent (5 yr). Flocks were allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

As shown in Figure 1 and Table 1, if flocks disengaged from sire referencing after 5 or 10 yr, flock r_{ij} continued to increase even though new physical connections between the flocks were no longer established. This same pattern can be observed in Figure 3, particularly when outside sires were not allowed. Bias no longer decreased after sire referencing stopped (Kuehn et al., 2007) even though flock r_{ij} continued to increase, resulting in a disparity with the anticipated relationship between bias and flock r_{ij} .

The relationship between flock PEVD and bias is shown for all scenarios in Figure 4. Points on the figure associated with lower values of flock PEVD coincided with more years of sire referencing. In general, as flock PEVD decreased, bias also decreased. However, unlike flock r_{ij} , the relationship between PEVD and bias is not consistent, especially between strategies where

outside rams were allowed or barred. Bias was lower, whereas flock PEVD remained higher when only homebred nonreference sires were used. At the same flock PEVD, bias was higher if outside sires were allowed. The inconsistency of this pattern raises questions regarding use of flock PEVD as a diagnostic measure to manage risk in across-flock genetic evaluations.

DISCUSSION

All of the connectedness measures followed expected patterns over 15 yr of selection within each scenario evaluated. The correlation measures increased as flocks participated in any form of sire referencing scheme and PEVD of EBV decreased. There were 2 possible reasons why these connectedness measures may have changed: a decrease in prediction error variance of animals or flock means, or a positive prediction error covariance between animals or their means. Prediction error variance decreases as more information becomes available to predict EBV. Based on Figure 2, connecting flocks through sire referencing schemes does reduce individual lamb prediction error, especially in small flocks with limited information within a single year (Smith and Banos, 1991). However, much of the gain observed in these connectedness measures came from prediction error covariances.

Prediction error covariance between animals is zero if no connections exist. Adding connections through related animals (due to use of reference sires in this study) or through direct contemporary comparisons causes the prediction error covariance between animals in separate flocks to increase. This positive covariance reflects a correlation between errors of breeding value predictions for pairs of animals, and these errors are more likely to be in the same direction. With correlated errors, bias between flocks should decrease as prediction error covariance increases.

Evaluating connectedness from the perspective of the current generation (i.e., lamb measures) had advantages and disadvantages. Lamb measures of connectedness (lamb r_{ij} and lamb PEVD) were more sensitive to changes in the design of breeding schemes than their counterpart flock-based measures. Immediately after flocks disengaged from sire referencing, the connectedness, as measured by lamb statistics, decreased. This sudden response can be attributed to lamb connectedness being measured only on the current generation rather than using historic data captured by the flock r_{ij} and PEVD. Individual lambs are not, on average, highly related to one another across flocks and do not have enough information to produce highly accurate EBV in the year their performance was first recorded. These lamb measures therefore assess the precision of comparing lamb EBV across flocks in the current year of evaluation and could be used to rapidly detect changes in between-flock mating systems. However, they do not effectively address the rate of removal

Table 2. Levels of average prediction error differences (PEVD; scaled by the additive variance¹) of lamb EBV and flock mean EBV after 5, 10, and 15 yr of selection under different types of sire referencing schemes and different levels of outside sire use

Source of nonreference sires	Breeding scheme	Lamb PEVD ²			Flock PEVD ²		
		5	10	15	5	10	15
Outside allowed	AI continuous	1.168	1.152	1.144	0.056	0.040	0.032
	AI 5 yr	1.168	1.248	1.276	0.060	0.052	0.056
	AI 10 yr	1.172	1.152	1.240	0.060	0.040	0.036
	AI sporadic	1.204	1.188	1.172	0.064	0.048	0.036
	NS ³ continuous	1.196	1.188	1.184	0.048	0.032	0.024
	No scheme	1.316	1.332	1.348	0.104	0.116	0.128
Homebred only	AI continuous	1.152	1.124	1.108	0.072	0.052	0.040
	AI 5 yr	1.152	1.236	1.288	0.072	0.072	0.080
	AI 10 yr	1.152	1.121	1.208	0.072	0.052	0.048
	AI sporadic	1.188	1.156	1.132	0.088	0.064	0.052
	NS continuous	1.180	1.168	1.156	0.060	0.044	0.032
	No scheme	1.372	1.416	1.460	0.156	0.192	0.228

¹PEVD are unitless measures because they have been divided by the additive variance.

²SE for lamb PEVD and flock PEVD were each < 0.003.

³NS = natural service.

over time in bias associated with differences in initial flock genetic means.

Lamb measures are highly dependent on pedigree relationships among lambs in different flocks. When large numbers of half-sibs were born each year in different flocks through AI sire referencing, lamb r_{ij} was high relative to natural service sire referencing for which lambs in different flocks were at most cousins. However, flock r_{ij} increased as rapidly (if not faster) in natural service referencing scenarios as compared with AI sire referencing scenarios, suggesting that mean flock EBV are effectively compared with natural service schemes even though lambs are not as highly related. With natural service, individual flocks both contributed and used more rams from other member flocks in the scheme, thereby establishing strong relationships among lambs across years. As a caveat, this result may not be general. In this study, the rams selected as reference sires, both for AI and natural service, were chosen from the top one-sixth on EBV. Reference sire use was also heavy in these small flocks with a majority of ewes mated to reference sires; heterogeneity in flock genetic means declined quickly once sire referencing began. As a consequence, most flocks both used and contributed rams to the reference sire pool. This mutual exchange of rams leads to strong connectedness.

Measures of connectedness involving flock means are based on the mean EBV of all animals within each flock. Therefore, they are functions of the accuracy of prediction of flock genetic means, which are the source of bias we are concerned about in this study. Both flock r_{ij} and PEVD therefore assess how well the model predicts differences in flock genetic means. Flock r_{ij} measures correlations in errors of predicted genetic means and flock PEVD measures the precision with which differences in genetic means are estimated. Because these measures are based on information on

whole flocks, they are less sensitive to changes in mating strategies between flocks and better reflect the monotonic decrease in bias observed by Kuehn et al. (2007) and in other simulation studies (e.g., Hanocq et al., 1996).

Flock r_{ij} was superior to flock PEVD in predicting patterns of change in percentage of bias explained over time. The general pattern in flock r_{ij} (Figure 3) was consistent regardless of the type of breeding scheme and whether homebred rams alone were mated to ewes not bred to reference sires. Some of the noise observed when outside sires were allowed was due to the decreased bias in the system after the 10 yr of random mating that occurred before group breeding schemes were initiated. Because the outside sires were drawn from a population with a common mean, flock genetic means regressed during the 10 yr of random mating and part of the bias simulated between flocks decreased (Kuehn et al., 2007). The amount of regression depended on the policy individual flocks adopted for use of outside rams, which varied between replicates of the simulation. This extra level of stochasticity, in addition to the sampling of flock genetic means, most likely accounts for the extra variance observed in Figure 3 for scenarios where outside sires usage was allowed.

The relationship of flock PEVD to bias, on the other hand, was highly dependent on the scenario, especially in terms of whether outside rams were allowed for nonreference sire matings. In all scenarios, bias decreased as flock PEVD decreased, but it was difficult to clearly define threshold values for PEVD to quantify the risk of comparing animals across flocks. The inconsistent pattern in PEVD relative to bias may partially be due to differences in inbreeding and average relationships within flocks in the 2 strategies used for mating surplus ewes. Because the relationship between animals within flocks must be higher when no

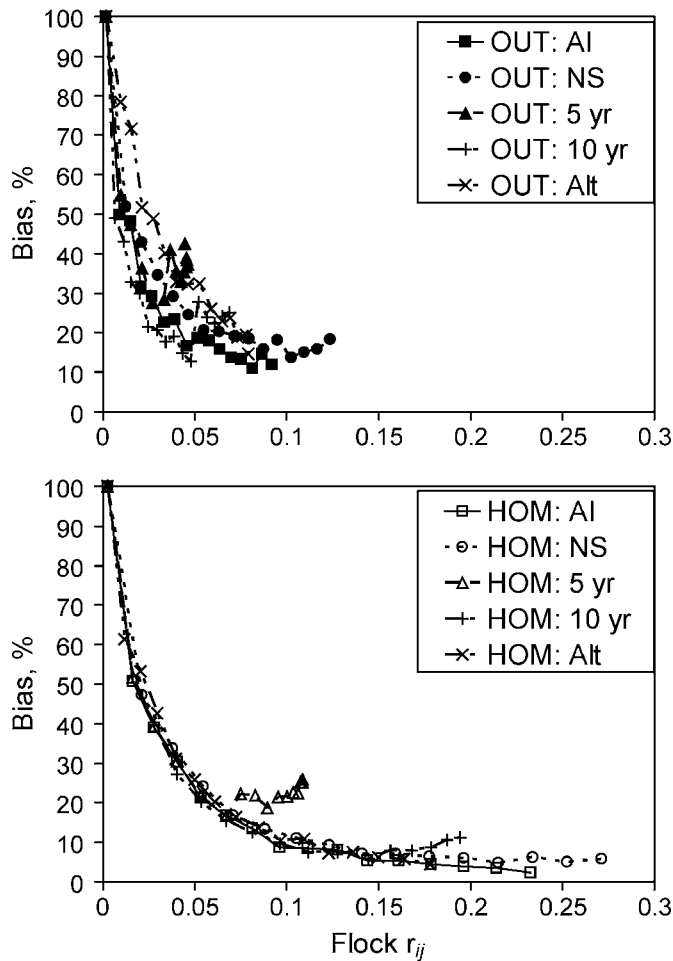


Figure 3. Average percentage of bias relative to flock connectedness correlation (r_{ij}) between 15 flocks over 15 yr of selection for different breeding schemes. Schemes are AI sire referencing (AI), natural service sire referencing (NS), sire referencing for 5 yr (5 yr), sire referencing for 10 yr (10 yr), and sporadic participation in sire referencing (Alt). Flocks were allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

nonpedigreed outside animals are brought into the system, the additive variance of mean comparisons across flocks should be higher, at least until connections are made between flocks. Although the values of the numerator relationship matrix were not available and could not be easily calculated with this level of replication, it may be useful to standardize flock PEVD using the average genetic relationship of animals between and within flocks as described by Laloë (1993).

The pattern for flock r_{ij} lends itself to possible benchmarks for management of risk due to different flock means. If 2 flocks achieve a flock r_{ij} level of 0.05, about 80% of bias due to differences in initial genetic means should be removed. Increasing flock r_{ij} to 0.10 should equate to a remaining level of bias equivalent to 10% of the initial level. These benchmarks can help producers

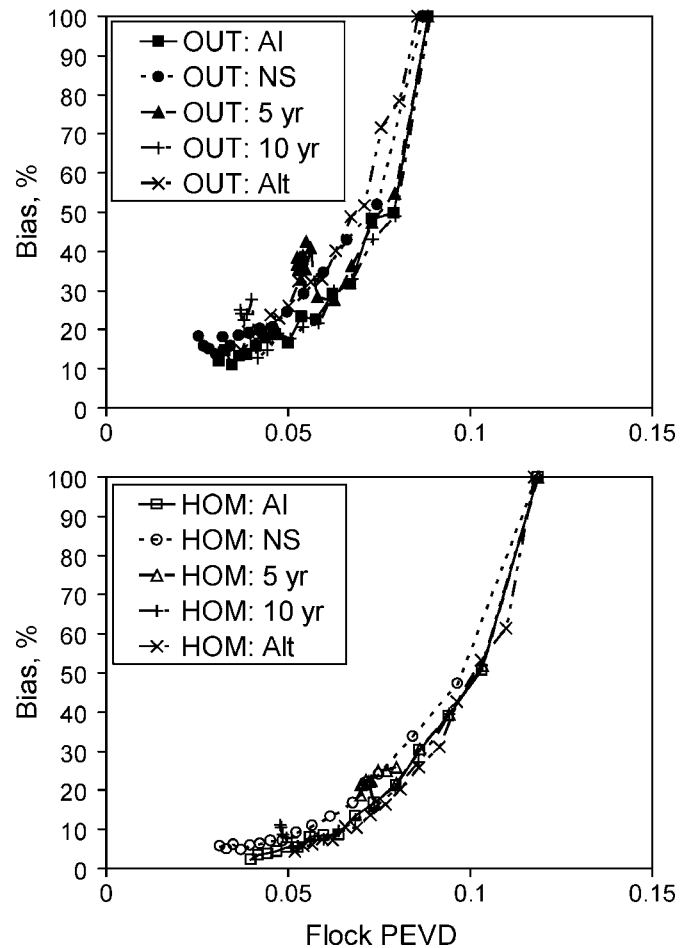


Figure 4. Average percentage of bias relative to the prediction error difference of mean flock EBV (PEVD) between 15 flocks over 15 yr of selection for different breeding schemes. Schemes are AI sire referencing (AI), natural service sire referencing (NS), sire referencing for 5 yr (5 yr), sire referencing for 10 yr (10 yr), and sporadic participation in sire referencing (Alt). Flocks were allowed to mate surplus ewes (those not mated to reference sires) to outside sires (OUT) or only to homebred sires (HOM).

decide whether further matings between flocks are desirable to further improve connectedness.

Establishing connections among flocks is important if the genetic means of flocks differ because biases in the genetic evaluation may otherwise occur. Connectedness measures can be increased with designed mating programs. The connectedness correlation of flock genetic means is the most consistent measure of the risk of bias in across-flock comparisons. Producers seeking to lower their risk when comparing the genetic merit of their animals to those in other flocks should enter into ram exchange programs and monitor connectedness using the flock connectedness correlation. Benchmark flock connectedness correlation values of 0.05 for good connectedness and 0.10 for superior connectedness will assist producers in deciding what level

of connectedness is sufficient to permit across-flock selection decisions.

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